

THE GENUS *LAEVICEPHALUS* (HOMOPTERA: CICADELLIDAE):
HOSTS, BIOGEOGRAPHY, AND THREE NEW SPECIES

ANDREW L. HICKS AND ROBERT F. WHITCOMB

Insect Biocontrol Laboratory, Plant Sciences Institute, Agricultural Research Service,
United States Department of Agriculture, Beltsville, Maryland 20705.

Abstract.—The genus *Laevicephalus* is comprised of small deltocephaline leafhoppers of North American grasslands. Although most species are southwestern and/or Mexican, some are northern or eastern. Southwestern species are largely associated with chloridoid (Poaceae: Chloridoideae) grasses. Some species are monophagous; others are oligophagous. Oligophagy coefficients are presented for 15 species of prairie and/or southwestern grasslands. Three new species are described: *L. warnocki* from chino grama (*Bouteloua ramosa*) in Big Bend National Park in Texas, *L. navajo* from montane blue grama (*B. gracilis*) grasslands of the Mogollon Rim and Sacramento Mountains of Arizona and New Mexico, and *L. nosabe* from side-oats grama (*B. curtipendula*) in Durango, Mexico.

Key Words: Leafhopper, grasslands, oligophagy, monophagy

The genus *Laevicephalus* DeLong is comprised of small, usually green leafhoppers that have speciated extensively in North American grasslands. Ross and Hamilton (1972) proposed a phylogenetic scheme that divided the genus into five species groups. Although the genus is especially diverse in southwestern and Mexican grasslands, some lineages occur primarily in northern and eastern grasslands. Extensive collections in the southwestern United States (Whitcomb et al. 1987, 1988, Lynn and Whitcomb 1987) have produced a large number of host records and biogeographic data on this genus. In this paper, we present host data for *Laevicephalus* species, and describe three previously unrecognized species.

HOST DATA

Host and biogeographic data on the genus *Laevicephalus* was accumulated in the course of a host-by-host, region-by-region sampling of grasslands (Whitcomb et al. 1987). Methods for collection (Whitcomb et al.

1986) and computerization of the accessions (Lynn and Whitcomb 1987) have been previously described. Oligophagy coefficients, computed as previously described (Whitcomb et al. 1987, Whitcomb and Hicks 1988), represent fractions of insects occurring on plant hosts at various (family, subfamily, genus, and species) levels. Oligophagy coefficients at the genus and species levels are presented in Table 1 for 15 species of *Laevicephalus* that appear to be relatively host specific. Some species, particularly those of more mesic and eastern grasslands, showed patterns that cannot be interpreted in terms of single host grasses. Eastern species with complex feeding patterns include *L. peronatus* Ross and Hamilton, *L. sylvestris* (Osborn and Ball), and *L. acus* (Sanders and DeLong). *L. tritus* Beamer and Tuthill, a southwestern species, was taken on a variety of grasses. *L. unicoloratus* (Gillette and Baker) is a characteristic species of tallgrass prairie, often feeding on *Andropogon* spp. or related warm-season grasses.

Table 1. Oligophagy coefficients (O_i) for the genus *Laevicephalus*.¹

<i>Laevicephalus</i> Species	Host Genus	O_{gen}	Host Species	O_{sp}	n
<i>aridus</i> Oman	<i>Bouteloua</i>	0.835 ¹	<i>eriopoda</i>	0.777	121
<i>curvus</i> Knull	<i>Eragrostis</i>	0.938	<i>trichodes</i>	0.938	16
<i>exiguus</i> Knull	<i>Bouteloua</i>	0.960	<i>gracilis</i>	0.356	101
			<i>hirsuta</i>	0.317	
<i>inconditus</i> Knull	<i>Bouteloua</i>	0.969	<i>curtipendula</i>	0.969	32
<i>melsheimerii</i> (Fitch)	<i>Danthonia</i>	1.000	spp.	1.000	68
<i>minimus</i> (Osborn & Ball)	<i>Bouteloua</i>	0.894	<i>curtipendula</i>	0.521	94
			<i>gracilis</i>	0.234	
<i>mexicanus</i> Ross & Hamilton	<i>Bouteloua</i>	0.973	<i>curtipendula</i>	0.973	37
<i>navajo</i> Hicks and Whitcomb	<i>Bouteloua</i>	0.866	<i>gracilis</i>	0.866	15
<i>obvius</i> Knull	<i>Bouteloua</i>	0.927	<i>gracilis</i>	0.588	330
<i>warnocki</i> Hicks and Whitcomb	<i>Bouteloua</i>	1.000	<i>ramosa</i>	1.000	70
<i>opalinus</i> Ross and Hamilton	<i>Bouteloua</i>	1.000	<i>gracilis</i>	0.836	73
			<i>curtipendula</i>	0.110	
<i>parvulus</i> (Gillette)	<i>Buchloë</i>	0.998	<i>dactyloides</i>	0.998	807
<i>salaris</i> Knull	<i>Distichlis</i>	0.921	<i>spicata</i>	0.921	126
<i>tritrus</i> Beamer and Tuthill	<i>Bouteloua</i>	0.512	<i>curtipendula</i>	0.433	82
<i>vannus</i> Knull	<i>Bothriochloa</i>	0.547	spp.	0.547	86

¹ Oligophagy coefficients (Whitcomb et al. 1987) represent the fraction of all insects collected on the indicated taxon. Only species for which adequate sample sizes are available are included in the analysis.

GEOGRAPHIC DISTRIBUTIONS

Despite our extensive surveys, the geographic distributions of many *Laevicephalus* species are still undetermined, since the ranges of many species extend into Mexico, where collection efforts have been inadequate. Some patterns are of particular interest. In Fig. 1, we present distributional records for four closely related *Bouteloua* specialists. Two of the species are strict specialists on side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.], whereas two others colonize blue grama (*Bouteloua gracilis* Willd. ex H.B.K.). In Fig. 2, we have mapped the type localities for species described herein.

DESCRIPTIONS OF NEW SPECIES

Laevicephalus warnocki Hicks and Whitcomb, NEW SPECIES (Figs. 2, 3)

Male.—Length, 2.24–2.68 mm, vertex length 0.16–0.27 mm, head width 0.67–0.79 mm, interocular width 0.24–0.32 mm. Head much wider than pronotum, crown narrow, bluntly rounded. Plates subtriangular, lined

laterally with uniseriate macrosetae. Styles evenly curved apically with inconspicuous denticulations (Fig. 3A). Aedeagus in lateral aspect (Fig. 3B) the same width throughout, slightly convex. In ventral aspect, shaft straight, with two pairs of processes, one pair apical, slender, recurved, subapical pair subtriangular with concave margins. Shaft apex broadly blunt, gonopore apical (Fig. 3D). Dorsal apodeme (= atrial arm) bisinuate, paralleling shaft, $\frac{2}{3}$ length of shaft. Pygofer elongate, exceeding plates, dorsally convex, slightly concave ventrally, with numerous scattered macrosetae.

Color stramineous; tegmina subhyaline, unmarked.

Female.—Length, 2.76–3.04 mm, vertex length 0.20–0.40 mm, head width 0.81–0.91 mm, interocular width 0.32–0.42 mm. Habitus similar to male, but with crown more produced and strongly angled, faint pair of arcs often present at apex. Seventh sternum (Fig. 3C) roundly produced, $\frac{2}{3}$ as long as broad, posterior margin weakly trilobed, median lobe slightly less produced than lateral lobes.

Color as in male.

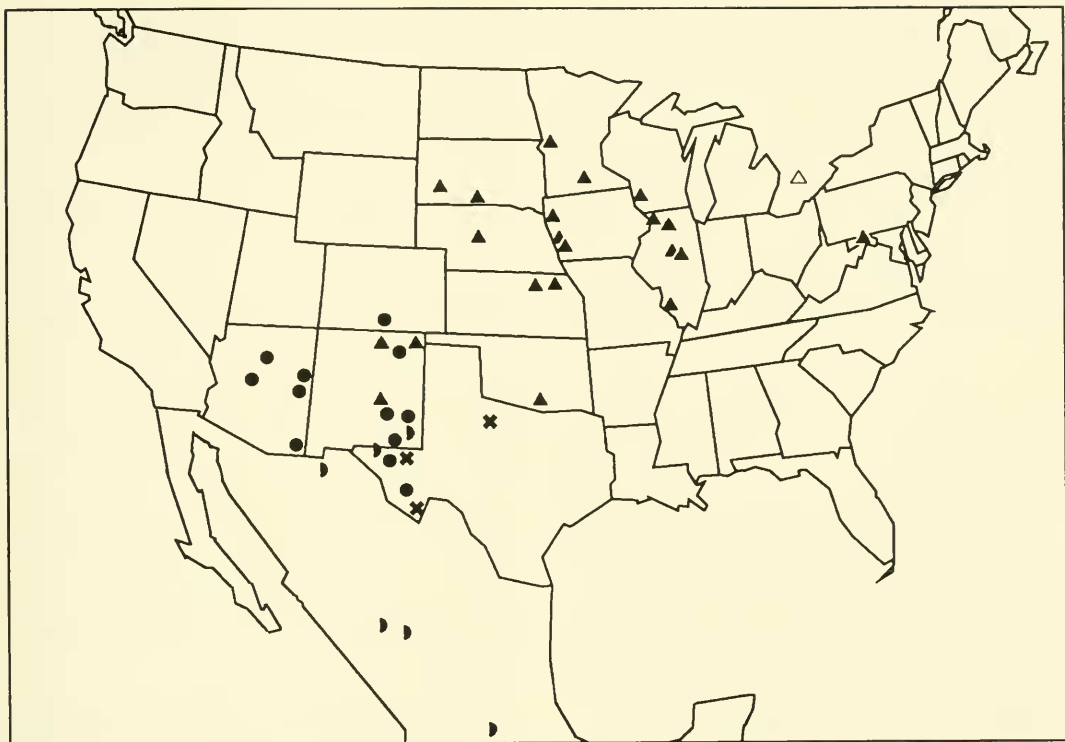


Fig. 1. Records for four species of *Laevicephalus* that specialize on *Bouteloua*. Two of the species occur mainly on side-oats grama (*Bouteloua curtipendula*). *Laevicephalus minimus* (▲ and △, the latter of which is a CNC record) is distributed throughout the true prairie, where it specializes on *Bouteloua curtipendula*. However, in the Colorado and New Mexico Rockies, it feeds on blue grama (*B. gracilis*). Another species, *L. inconditus* Knull (×) occurs in Chihuahuan grasslands, and *L. opalinus* (●), which more often occurs on blue than side-oats grama, is distributed in Southwestern grasslands west of the Chihuahuan region. *Laevicephalus mexicanus* (◐), previously known only from near Mexico City, has been collected on side-oats grama in southeastern New Mexico, a region in which all four of these species occur.

Type material.—*Holotype male*: Texas: Brewster Co., Big Bend National Park, Panther Junction, 26 August, 1985, 3500 ft, R. F. Whitcomb and A. L. Hicks, IPL 002081, on *Bouteloua ramosa* Vasey, deposited in NMNH, Washington, D.C. *Paratypes*: Texas: Big Bend National Park, same data as holotype, IPL 002081, 82, and 83, 25 males, 6 females. Texas: Big Bend National Park, Chisos Mtns., 5000 ft, August 4, 1984, R. F. Whitcomb and A. L. Hicks, IPL 000818, 1 male; Texas: Big Bend National Park, 2600 ft, August 25, 1985, IPL 002055, 8 males, 3 females. Deposited in BARC, Beltsville, Maryland; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa, Ontario; Kansas University,

Snow Museum, Lawrence; Kansas State University, Manhattan; Monte L. Bean Museum, Brigham Young University, Provo, Utah; Ohio State University, Columbus; and NMNH.

Diagnosis.—The male genitalia of *L. warnocki* are similar to those of *L. salarius* Knull, to which it keys in the treatment of Ross and Hamilton (1972), and *L. canyonensis* Knull. However, *L. warnocki* can be differentiated from both of these species by the morphology of the subapical processes, which in ventral view have a straight anterior margin. Also, *L. canyonensis* is readily separable from *L. warnocki* and *L. salarius* on the basis of its coronal stripes.

Host.—This species has been collected

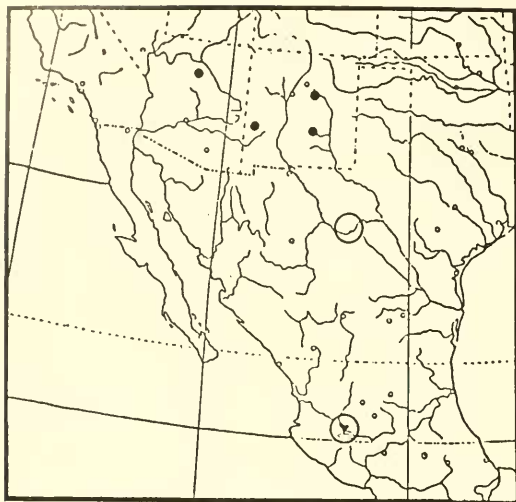


Fig. 2. Localities for new species. Large dots are localities for *L. navajo*, open circle for *L. warnocki*, and circle with inverted triangle for *L. nosabe*.

only in Big Bend National Park, where it apparently specializes on chino grama, *Bouteloua ramosa*.

Etymology.—We have named this species for Dr. Barton Warnock, who assisted us in many ways with the botany of trans-Pecos Texas.

***Laevicephalus navajo* Hicks and
Whitcomb, NEW SPECIES**
(Figs. 2, 4)

Male.—Length, 3.0–3.36 mm, vertex length 0.36–0.40 mm, head width 0.88–0.97 mm; interocular width 0.32–0.44 mm. Head much wider than pronotum, anterior margins straight, apex acute. Plates subtriangular, lined laterally with uniseriate macro-

setae. Style apices evenly curved laterad, apical denticulations inconspicuous or absent (Fig. 4A). Aedeagus in lateral aspect (Fig. 4B) strongly arched, tapering gradually toward apex. In ventral aspect (Fig. 4D), shaft narrow and straight, abruptly widened to pair of acute retrorse processes (Fig. 4D); shaft bluntly rounded with slight medial indentation; gonopore ovoid, subapical on ventral surface of shaft (Fig. 4C). Dorsal apodeme paralleling shaft, attaining $\frac{1}{2}$ length of shaft, recurved apically. Pygofer elongate, exceeding plates, dorsally flattened, slightly concave ventrally, with numerous scattered macrosetae.

Tawny brown or fulvous, tegmina semi-hyaline but with cells margined widely with dark brown. Crown with variable markings with apical dark brown arcs. Face tawny and unadorned, marked with brown transverse lines.

Female.—Length, 3.36–4.04 mm. Vertex length 0.36–0.48 mm; head width 0.88–0.99 mm, interocular width 0.36–0.48 mm. Habitus as in male. Seventh sternum (Fig. 4D) with posterior margin wedge-shaped with slightly embrowned blunt apex.

Color as in male.

Type material.—*Holotype male*: Arizona: Coconino Co., Red Lake (north of Williams), 6400 ft, 13 Sept., 1986, R. F. Whitcomb, IPL 002714, on blue grama (*Bouteloua gracilis*), deposited in NMNH. *Paratypes*: Same collection data as holotype, 1 male, 3 females; New Mexico: Lincoln Co., Ft. Stanton, 7600 ft, 9 Sept. 1987, R. F. Whitcomb, IPL 003536, on *Muhlen-*

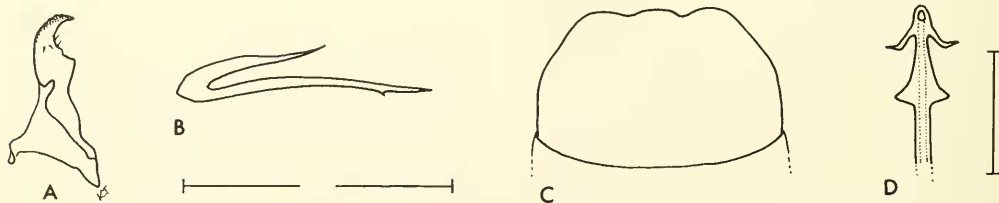


Fig. 3. *Laevicephalus warnocki* Hicks and Whitcomb n. sp. (Scale lengths in parentheses.) A. Style, broad aspect (0.5 mm); B. Aedeagus, lateral aspect (0.5 mm); C. Female sternum VII (0.5 mm); D. Apex of aedeagus, detail, ventral aspect (0.1 mm).

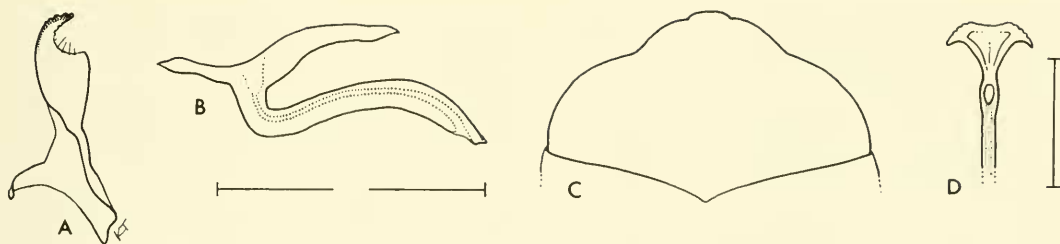


Fig. 4. *Laevicephalus navajo* Hicks and Whitcomb n. sp. (Scale length in parentheses.) A. Style, broad aspect (0.5 mm); B. Aedeagus, lateral aspect (0.5 mm); C. Apex of aedeagus, detail, ventral aspect (0.1 mm); D. Female sternum VII (0.5 mm).

bergia pauciflora Buckl., 1 male, 1 female. New Mexico: Sante Fe Co., Edgewood, 6600 ft, 29 August 1987, R. F. Whitcomb, IPL 003390, on *B. gracilis*, 3 males, 2 females, 1 immature; New Mexico: Catron Co., Aragon, 7340 ft, 16 August, 1987, IPL 001759, A. L. Hicks, on *B. gracilis*, 1 male; New Mexico: San Miguel Co., Villanueva, 6000 ft, 13 Aug. 1987, IPL 001745, on *B. gracilis*, A. L. Hicks, 1 male. Deposited in NMNH, Washington, D.C.

Diagnosis.—*L. navajo* can be distinguished from all other members of the genus by its dark brown color. It will key (Ross and Hamilton 1972) to *L. vannus* Knull, but can be distinguished from this species by the decurved, laterally compressed aedeagus. The morphology of its male genitalia suggest that it is a sister species to *L. longus* Knull, from which it can be distinguished by the configuration of the aedeagal apex.

Host.—This species has been collected in

Arizona and New Mexico from chloridoid grasses, especially *Bouteloua gracilis*. However, its relative scarcity in many accessions from this grass, even within its range, suggests complex habitat requirements.

Etymology.—We have named this species for the Navajo tribe of Native Americans, upon whose lands (in part) this species occurs.

***Laevicephalus nosabe* Hicks and Whitcomb, NEW SPECIES**
(Figs. 2, 5)

Male.—Length, 2.92–3.00 mm, vertex length 0.28–0.36 mm, head width 0.80–0.84 mm, interocular width 0.32–0.36 mm. Head much wider than pronotum, crown narrow, anterior margins straight, apex acute. Plates subtriangular, lined laterally with uniseriate macrosetae. Styles in broad aspect curved laterad to truncate dentate apex (Fig. 5A). Aedeagus in lateral aspect (Fig. 5B) narrow,

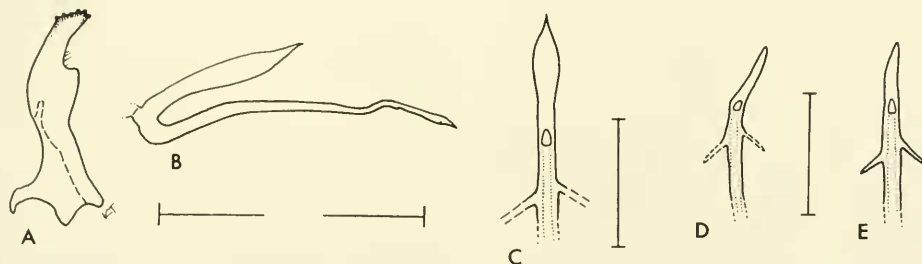


Fig. 5. *Laevicephalus nosabe* Hicks and Whitcomb n. sp. (Scale length in parentheses.) A. Style, broad aspect (0.5 mm); B. Aedeagus, lateral aspect (0.5 mm); C. Apex of aedeagus, broad aspect (0.1 mm); D. same, showing broken processes (0.1 mm); E. same, showing processes entire (0.1 mm.).

weakly arched, with straight midsection and decurved apex. In ventral aspect, aedeagus straight, curving and twisting slightly in distal quarter, curving slightly dextrad. Two tiny retrorse processes (broken in one specimen, Fig. 5D), the right slightly distad from the left in ventral broad aspect (Fig. 5E), occurring at $\frac{1}{2}$ the shaft length from the apex. Dorsal apodeme $\frac{1}{2}$ length of shaft and slightly divergent. Gonopore minute, preapical, on ventrolateral surface; aedeagal apex (Fig. 5C) diamond-shaped distad of the gonopore, slightly wider than shaft, and dorsoventrally flattened. Pygofer with shallow indentation on ventral surface dorsad of lateral lobe of style, with scattered macrosetae.

Head and pronotum bright yellow-green to pale green. Crown with fuscous arcs at apex, otherwise unmarked.

Female.—Unknown.

Type material.—*Holotype male*: Mexico: Durango, 24.5 mi southeast of Durango, 6.5 mi west of Nombre de Dios, Mexican Highway 45, 6400 ft, Oct. 1, 1988, A. L. Hicks, IPL 002822, deposited in NMNH. *Paratypes*: 2 males, same collection data, deposited in NMNH.

Diagnosis.—The male genitalia of *L. nosabe* are similar to those of *L. ustulatus* Ross and Hamilton, from which *nosabe* can be differentiated by the configurations of the aedeagal apices. The aedeagal spines in *nosabe* are more developed. The diamond-shaped apex of the aedeagus, which is widest beyond the apical processes, distinguishes *nosabe* from all other members of the *tritus* species group, and particularly, from *tritus*, to which it will key in the treatment of Ross and Hamilton (1972).

Host.—The type series was collected from a mixed association of grasses in which side-oats grama, *Bouteloua curtipendula*, was dominant.

Etymology.—The Spanish “no sabe,” used to express doubt or lack of knowledge, seemed appropriate for this species, which is—like so many Mexican species represented by only a few specimens—enigmatic.

DISCUSSION

Availability of phylogenies for the genera *Flexamia* DeLong (Whitcomb and Hicks 1988) and *Athysanella* Baker (Blocker and Johnson 1988, Blocker and Johnson 1990a, b) has permitted a preliminary analysis of the biogeography and evolutionary history of those genera (Whitcomb et al. 1990). The preliminary phylogeny of Ross and Hamilton (1972) suggests that two relatively small lineages of the genus (the *sylvestris* and *poudris* groups) evolved in northern and/or eastern grasslands. Two groups (*parvulus* and *minimus*), like *Flexamia* and *Athysanella*, clearly evolved with warm-season grasses in the American Southwest and Mexico. The preliminary phylogeny should be revised to include currently known species, including those described herein and *L. satchkatchewanensis* Hamilton and Ross (1975) by objective analysis.

Geographic records for *Laevicephalus* suggest that distributions of many species are partly or largely Mexican. Many of the species appear to occur throughout the Mexican highlands from Mexico DF into the southwestern United States. Further acquisitions from Mexico would clearly improve our understanding of this genus.

The host records presented in Table 1 suggest that some *Laevicephalus* species are highly host specific. On the other hand, there is a clear tendency for host specificity of grassland cicadellids to be much more pronounced in northern parts of their range (Whitcomb et al. 1987). It is therefore especially important that host records be obtained from the southern periphery of the range of *Laevicephalus* species, where they may have more generalized host selection.

The host affinities of the species depicted in Fig. 1 is of special interest. All are members of the *minimus* subgroup, a monophyletic clade identified by Ross and Hamilton (1972). All feed on side-oats grama, but two species also feed on blue grama, and one of these occurs most often on blue grama. It is possible that the forms of *L. minimus* (Osborn and Ball) found in the Rockies on

blue grama, apparently allopatric with the eastern side-oats forms, are a cryptic species. The division of *L. opalinus* Ross and Hamilton into cryptic but sympatric specialists of the two gramas appears less plausible. Although intrageneric crossovers are frequently encountered in host relationships of grass-feeding leafhoppers, blue and side-oats grama are extremely different in growth form and floral morphology. Other leafhopper genera, such as *Flexamia* and *Laevicephalus*, make this crossover rarely if ever. Perhaps the ability of *minimus* and *opalinus* to make this crossover reflects a long tenure of the lineage in the mixed *Bouteloua* grasslands of northern Mexico and the American Southwest.

A thoughtful revision of this genus, and a comparison of its evolutionary history with other genera, would improve the understanding of the ecology and evolution of insects in southwestern grasslands.

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